

Intrafamilial Relationships of the Thelypteroid Ferns (Thelypteridaceae)

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ABSTRACT.—Data from three chloroplast genes (*rps4* + *trnS* spacer, + *trnL* spacer; 1350 base pairs) for 27 of the recognized segregates show the Thelypteridaceae to be monophyletic and sister to an unresolved alliance of blechnoid, athyroid, onocleoid, and woodsoid ferns. The family comprises two primary lineages, one phegopteroid, the other thelypteroid (including cyclosoroid). The phegopteroid lineage (*Macrothelypteris*, *Pseudophegopteris*, and *Phegopteris*) includes those elements that are the most dissected, lack adaxial grooves on the frond axes, and are generally morphologically the most distinct elements within the family. Within the thelypteroid-cyclosoroid lineage, three predominantly north-temperate subgroups, including *Thelypteris* s.s., form a free-veined clade that is in turn sister to the rest of the family. All segregates possessing $x=36$ (*Cyclosorus* sensu Smith, with predominantly anastomosing veins) form a strongly supported clade. Those groups with dysploid base chromosome numbers ($x=27, 29, 30, 31, 32, 33, 34, 35$) form a series of smaller clades basal to *Cyclosorus* s.l. Although our sampling is not yet sufficient to favor one classification over another, recognition of an intermediate number of genera may be the most reasonable taxonomic course.

Since its taxonomic separation from the dryopteroid ferns as a distinct group, about 60 years ago, Thelypteridaceae has been treated as a natural group comprising nearly 1000 mostly tropical species. Although generally recognized as a natural monophyletic group, there is a wide divergence of views about generic circumscription. Morton (1963) placed all species in a single genus *Thelypteris*. Ching (1963) outlined a classification that accepted 18 Asian genera, including *Hypodematum*, which is generally excluded from the family by other workers, even by Ching (1978). Ching (1978) later added two newly described genera to Thelypteridaceae: *Craspedosorus* (which we regard as a synonym of *Leptogramma*, often included in *Stegnogramma* sensu Iwatsuki, 1963); and *Trichoneuron* (regarded by us as belonging to *Lastreopsis*, a dryopteroid, definitely not thelypteroid). Both of these genera are monotypic and poorly known. Still later, Shing (1999), subsumed *Amphineuron* under *Cyclosorus* s.l. and removed *Trichoneuron* from the family. Iwatsuki (1964) recognized three genera in the family, *Stegnogramma* and *Meniscium* (each with four sections), and *Thelypteris*, the last comprising 14 subgenera and several additional sections; Iwatsuki (1964:23) regarded two of his subgenera of *Thelypteris* (*Haplodictyum* and *Cyrtomiopsis*) as probably “generically distinct.” Holttum (1971, 1982) characterized 25 genera in the Old World but did not explicitly address New World groups. Pichi Sermolli (1977:335–337), largely following Holttum, accepted 32 genera. In the most recent classification, Smith (1990) adopted an intermediate view, recognizing